

The changing ecology of tropical forests

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The threat to tropical forests is often gauged in terms of deforestation rates and the total area remaining. Recently, however, there has been a growing realization that forest can appear intact on a satellite image yet be biologically degraded or vulnerable to degradation. The array of direct threats to humid tropical forest biodiversity, in addition to deforestation, includes: selective extraction of plants; selective extraction of animals; biological invasion; fragmentation; climate change; changing atmospheric composition; and increasing tree turnover rates. The threats are linked to one another by a poorly understood network of causality and feedback effects. Moreover, their potential impacts on forest biodiversity are hard to assess because each threat is as likely to precipitate indirect effects as direct effects, and because several threats are likely to interact synergistically with one another. In spite of the uncertainties, it is clear that the biological health of tropical forests can become seriously degraded as a result of these threats, and it is unlikely that any tropical forest will escape significant ecological changes. Some groups of plants and animals are likely to benefit at the expense of others. Species diversity is expected to decline as a consequence of the changes in forest ecology. In the 21st century scientists and conservationists will be increasingly challenged to monitor, understand, prevent and head off these threats.

Keywords: biodiversity; degradation; defaunation; fragmentation; climate change; carbon fertilization; increasing turnover; interactions; monitoring.

Introduction

Most land in the tropics has some history of human use (Flenley, 1979; Sanford *et al.*, 1985; Balée, 1989, 1994; Horn and Sanford, 1992). These human activities, such as hunting and deforestation, were once very restricted in time and space. Therefore, defaunated areas were usually recolonized and deforested clearings usually regenerated. However, with technological and population expansion, the same activities are now becoming increasingly pervasive, giving tropical forests less opportunity to recuperate.

Satellite images present one, very graphic, view of the spreading threat. They show that large-scale deforestation is proceeding in many parts of the tropics (Myers, 1989, 1993; FAO, 1993; Grainger, 1993; Skole and Tucker, 1993). Less than half the original extent of tropical forests remains in primary forest, so deforestation must have already set in train a massive wave of extinction (Myers, 1988; Sayer and Whitmore, 1991). Yet outright clearing of the forest is only one, albeit the most extreme, among a series of changes that are affecting the ecology of the earth's most diverse ecosystems. The other changes will not necessarily remove forest cover. Instead, they are more likely to cause progressive degradation of forest structure and biodiversity. Unlike the obvious devastation caused by clear-felling or large fires, these other threats share the quality of being hard to perceive without careful monitoring. (Only one, fragmentation, is potentially visible with satellite

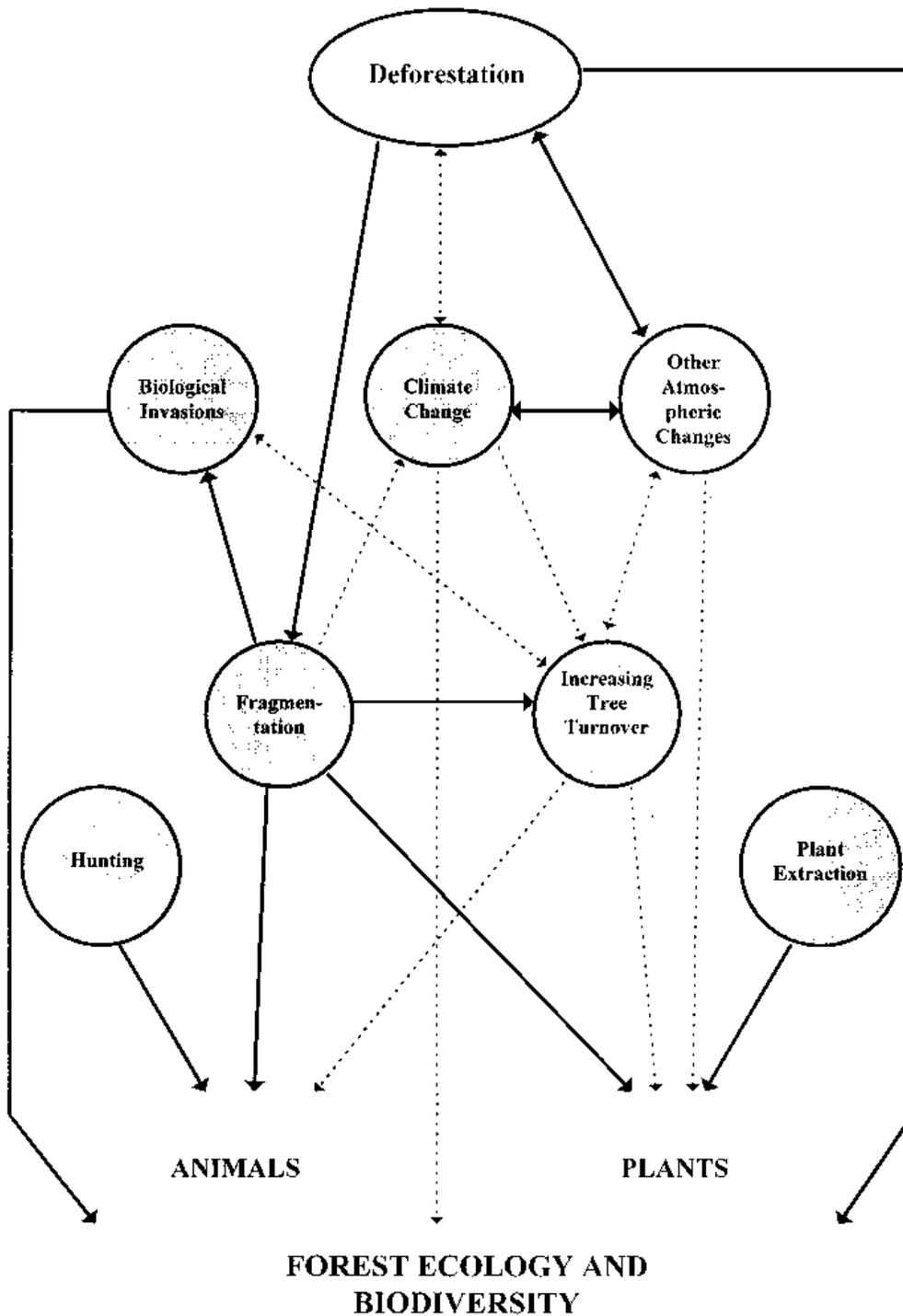
imagery, and the cascade of knock-on effects following fragmentation cannot be perceived by remote sensing.) These threats to forest biodiversity are additionally disquieting for conservationists because they will not operate in isolation, but rather may coincide with one another and with the dominant threat posed by deforestation. Therefore, in some cases we can expect that the threats will interact synergistically to magnify their impact on forests.

Recent geographical work has developed a framework for classifying the complex nature of tropical forest degradation from a cultural biogeographic perspective (Grainger, 1996). But forest degradation is also a biological process, so we also need to understand the ecology of changing forests. So far, biologists have mostly only examined the impacts of individual degradatory processes – particularly fragmentation (e.g. Wilcove, 1987; Saunders *et al.*, 1991), climate change (e.g. Hartshorn, 1992), and defaunation (e.g. Redford, 1992). In this paper I attempt to develop a broader biological approach to the degradation of humid tropical forests by considering the full spectrum of the forest degradation threats from a biocentric perspective and exploring some of the links between different agents of degradation.

Non-deforestation threats to tropical forest biodiversity can be considered in seven distinct categories: (a) selective extraction of plants; (b) selective extraction of animals; (c) biological invasion; (d) fragmentation; (e) climate change; (f) changing atmospheric composition; and (g) changing tree turnover rates. Each phenomenon merits serious consideration as an agent of change in the ecology of tropical forests. Nevertheless, the seven threats are extremely diverse and defy simple classification. The first two represent an obvious immediate bodily removal of plants and animals, followed by a much less obvious and potentially more significant series of indirect ecological effects on the remaining biodiversity. Biological invasions (c) may initially increase local diversity, but eventually lead to extinctions caused by direct and indirect ecological effects. Threats (d), (e), (f) and (g) might also have immediate direct impacts on organisms, but more importantly they also involve changes to the wider physical environment which will alter the long-term ability of the forest to maintain natural levels of biodiversity. Finally, threats (c) through (g) are themselves partly or wholly higher products of other forest threats. Indeed, most of the seven threats are affected by other threats, including deforestation, in a complex and poorly understood web of feedback effects. Figure 1 represents a simplified model of the known and hypothetical links among the threats.

The central questions addressed here are: ‘What are the biological implications of each of these degradatory processes?’, and ‘How might interactions and feedback effects modify the biological responses to the processes?’. To answer these questions, I first present a brief overview of the threats of tropical forest biodiversity. Two particular threats (defaunation and increasing tree turnover) are then discussed in more detail, as they provide instructive

Figure 1. Schematic chart of interactions among factors threatening tropical forest biodiversity and ecology. Thick lines represent known effects, dashed lines represent potential effects. The figure distinguishes direct effects on plants from direct effects on animals where possible, but does not attempt to model the plant – plant, plant – animal, and animal–animal interactions that will determine the ultimate effects on biodiversity of each threat. ‘Deforestation’ includes clear-felling, as well as intensive logging, and human-caused fires that removes the forest cover. ‘Biodiversity’ represents the species-level and ecosystem-level diversity.



examples of the potential for indirect effects to alter tropical forest ecology in unexpected ways. Finally, I explore the potential for synergisms among threats, and the conservation implications of biotic degradation.

Overview of threats

The individual threats are briefly summarized here, with an outline of each threat and tropical examples of likely direct and indirect impacts on plants and animals. Where appropriate, the summaries and examples also consider likely synergistic interactions with other threats.

SELECTIVE EXTRACTION OF PLANTS

General

Almost any plant species may be the target of extraction, and primary forest is often utilized for a wide variety of both subsistence and commercial uses (Phillips *et al.*, 1994a). Exploitation can involve rapid, non-sustainable harvesting of particular species (Gentry and Vásquez, 1988), leaving behind a standing but biologically and economically depleted forest. Except for heavy selective logging (Myers, 1989), this form of resource use rarely results in obvious structural changes, and therefore extractive forest is typically indistinguishable from pristine forest on satellite images. National forest assessments that do not include extensive ground-truthing by local experts may wrongly assume that forests are intact when in reality they have already been mined of economically valuable plants.

Direct effect examples

Extraction of individual timber trees has left species like *Swietenia macrophylla* (mahogany) and *Cedrela odorata* (South American cedar) extinct across most of their former range, even in areas still maintaining 100% forest cover. Several fruit trees and medicinal plants are also extinct in most forests within 100 km of the small Peruvian city of Iquitos, since it is often easier to cut trees for their fruit or latex than to climb or tap them (Padoch, 1988; Vásquez and Gentry, 1989).

Indirect effect examples

Where only scattered individuals or populations survive harvesting, species may be vulnerable to inbreeding, leading to further declines in genetic diversity. Extinctions can be anticipated among other forest plants and animals (e.g. pollinators, fruit-dispersers) if they depend on the over-harvested economic species for their own survival. If extractive logging substantially alters the forest structure, humid tropical forest may become susceptible to fire.

REMOVAL OF ANIMALS ('DEFAUNATION')

Very few tropical forest areas now have pristine assemblages of mammals and birds. Surprisingly low population densities of humans can devastate a fauna, both directly (for example, by subsistence hunting) or indirectly (for example, by removing many species' critical food supplies by cutting fruit trees). Later I will explore the consequences of such direct effects on the fauna, and indirect effects on the flora and fauna.

BIOLOGICAL INVASIONS

General

Exotic plant and animal species are important factors in causing extinctions, particularly among endemic species on remote islands (e.g. Vitousek, 1988; Simberloff, 1992; Cronk and Fuller, 1996). Invading plant species typically have superior competitive abilities to the native species, and invading predators may wipe out native herbivores that have little ability to defend themselves. In more continental settings most communities are less susceptible to invasion, although disturbance to the natural vegetation can still facilitate invasion by competitive alien species.

Direct effect examples

In primary wet forest on Mauritius, a few exotic plant taxa (*Psidium*, *Ligustrum*, *Ardisia*) constitute most of the seedling individuals and threaten to completely take over the forest (Lorence and Sussman, 1986). In the Hawaiian archipelago, predation by introduced rats may have precipitated the extinction of several endemic birds (Atkinson, 1977).

Indirect effect examples

When island birds are extirpated by rats, cats or humans, endemic plant species may lose their natural fruit dispersal agents. Even in intact continental ecosystems, alien species can have substantial impacts: rainbow trout (*Oncorhynchus mykiss*) have become top predators in some east Andean montane forest streams, indirectly modifying both the diversity and the trophic structure of forest streams and rivers (Young *et al.*, 1994).

FRAGMENTATION

General

Spatial aspects of fragmentation are typically visible and quantifiable from satellite imagery (Skole and Tucker, 1993; Grainger *et al.*, 1996). However, subsequent ecosystem decay in isolated fragments (Wilcove, 1987; Terborgh, 1992) is largely invisible from above as fragments can acquire a simpler biological state without obvious changes in vegetation structure and canopy reflectance. Other things being equal, larger fragments support more species than smaller fragments (MacArthur and Wilson, 1967; Dale *et al.*, 1994), but even the largest existing forest reserves may be inadequate to protect all their species (Thiollay, 1989).

Direct effect examples

Species occurring at very low densities over large areas may be especially vulnerable to local or global extinction as a result of reductions in their total available habitat. Also, since tropical forest regions can contain numerous, distinct biological communities (Tuomisto *et al.*, 1995), those species that specialize in restricted environments will be prone to extinction as a result of random sampling error when larger areas become subdivided.

Indirect effect examples

After isolation, a number of interacting processes, including loss of genetic diversity and greater vulnerability to natural catastrophes, may threaten species' long-term survival. Small fragments, or fragments with high fractal dimension, will be especially vulnerable to edge effects, although the nature and penetration of forest edge habitat into the forest

interior will vary greatly from species to species (Williams-Linera, 1990). The potential variety of edge effects that may impact the forest is almost infinite, including vegetation desiccation (Kapos, 1989), higher rates of tree mortality and therefore of gap formation (Lovejoy *et al.*, 1984), greater exposure to hunting pressure and other threats such as heavy seed rain from weedy species – alien or native – growing in adjacent secondary vegetation (Janzen, 1983, 1986; Simberloff, 1992; Turner and Tan, 1992; Turner *et al.*, 1994).

CLIMATE CHANGE

General

Recent work suggests that tropical climates may be very susceptible to global climatic changes. In the last ice-age, temperatures in the tropics may have been $\geq 5^{\circ}\text{C}$ cooler than today (e.g. Bush *et al.*, 1993; Guilderson *et al.*, 1994; Stute *et al.*, 1995). In the warmer world of the near future, outer tropical forests are likely to experience more frequent and more powerful hurricanes (O'Brien *et al.*, 1992) and most tropical regions will experience greater seasonal extremes between wet and dry seasons. Seasonality is known to be a principal determinant of vegetation type, species richness, and biological activity in the tropics (Foster, 1982; Hartshorn, 1992; Clinebell *et al.*, 1995).

Regional environmental changes may also have a climatic impact. Tropical rainfall depends partly on evapotranspiration from standing forest (Meher-Homji, 1991; Salati and Nobre, 1991), so that deforestation might lead to regional climate changes that desiccate forests, accelerating forest decline. Climate changes have been documented in several tropical regions that have been substantially deforested (e.g. Zhang, 1986; Windsor, 1990), but a link between the two processes is far from proven.

Direct effect examples

Increasing seasonality of climate could benefit species physiologically pre-adapted to live in more seasonally arid forests (e.g. some reptiles, Bromeliad epiphytes, and small-leaved deciduous vines with tubers) at the expense of those requiring year-round humid environments (e.g. some amphibians, some fern epiphytes, and evergreen vines with large leaves). A change to drier climatic conditions in central Panama has coincided with sharp population declines in small tree and shrub species that specialize in moist microhabitats, and at least 16 species are predicted to become locally extinct in a 50 hectare inventory plot (Condit *et al.*, 1996).

Indirect effect examples

As a result of deforestation and fragmentation, in the next century there will be few large unbroken areas of trans-altitudinal and trans-latitude forest. This will be a critical factor in distinguishing the biological impact of future rapid global change from that of past natural changes. Many plant and animal populations will be unable to track their optimal climate by migrating across future landscapes. Montane forests may be most severely impacted of all, since their lower limits may be forced upward by warmer and drier climates and their upper limits will be unable to advance in the face of human activities. By the standards of tropical forests, montane forests are not unusually diverse but they do contain a very high proportion of narrow-range endemic plants and animals (Young, 1992; Gentry, 1995; Jorgensen *et al.*, 1995). Climate change, in concert with deforestation and fragmentation, therefore presents a very serious threat to the survival of many species.

OTHER ATMOSPHERIC CHANGES

General

Carbon dioxide is not only a greenhouse gas, but also a basic plant nutrient used by plants during photosynthesis. The increasing concentrations of atmospheric carbon dioxide will directly affect plant metabolism everywhere (e.g. Condon *et al.*, 1992; Johnson *et al.*, 1993). Other atmospheric changes are less globally pervasive, but tropospheric ozone pollution, acid rain, smoky atmospheres from fires, and nutrient deposition from smoke, will all have local impacts on forest metabolism and may precipitate knock-on effects on forest composition.

Direct effect examples

The increase in atmospheric CO₂ levels has already had a biological impact. It is known to have caused: reductions in the number of leaf stomata in some temperate species (Woodward, 1987, 1992; Beerling and Woodward, 1993); increases in water-use efficiency (Wayne Polley *et al.*, 1993); and possibly an increased cambial growth rates in temperate trees (Graybill and Idso, 1993). Increasing CO₂ is likely to directly benefit intrinsically fast-growing species (e.g. Condon *et al.*, 1992) because they are pre-adapted to exploit high-resource environments.

Indirect effect examples

It is difficult to predict how these metabolic changes will affect tropical forests, but we can expect impacts on ecosystem-level processes and therefore ultimately on the species composition and diversity of ecosystems (Bazzaz, 1990; Woodward, 1992; Johnson *et al.*, 1993). The ratio of carbon to nitrogen in litterfall may increase, which would favour some detritivorous animal and fungal species over others and perhaps slow overall decomposition rates.

CHANGING TREE TURNOVER RATES

For unknown reasons, possibly related to one or more of the above anthropogenic impacts, inventory plot data suggest that the rate at which trees are dying and being replaced in mature tropical forests has increased (Phillips and Gentry, 1994). Increasing turnover will almost certainly have impacts on biodiversity, as will be discussed later.

Two invisible threats

Defaunation and changing turnover are discussed here in more detail. They are both 'invisible' processes, i.e. not visible on remotely-sensed images and therefore perceived only by careful ground monitoring. Direct, indirect, and feedback effects of both phenomena could create surprising and profound changes in the ecology of tropical forests.

DEFAUNATION

A few human hunters can defaunate a large area (Yost and Kelley, 1983; Thiollay, 1989; Peres, 1990). The largest primates like *Ateles* (spider monkeys) and *Lagothrix* (woolly monkeys), and some large cats, caimans, raptors, macaws and game-birds, are effectively extinct in large parts of Amazonia (Thiollay, 1989; Peres, 1990). Many other animal

species are also depleted by hunting. The 'empty forest' (Redford, 1992) is an apt characterization for the vast tracts of ostensibly pristine forest which have had many mammal and bird populations hunted out. Moreover, most tropical rivers are fished and many are over-exploited; this too may affect forest ecosystems since some fish species are important seed dispersers in seasonally flooded forests (Goulding, 1980; Kubitzki and Ziburski, 1994).

Human predation is having an obvious direct impact on the hunted forest animals. But since ecological communities are characterized by a complex web of interactions among species, we can expect indirect effects to propagate through the ecosystem, almost certainly having effects on plants and animals not obviously connected to the target species. Few studies have attempted to trace how the indirect effects of defaunation propagate through the community, but it is already clear that defaunation can cause progressive change in the forest community toward a simpler state. However, most plants have longer life-cycles than most animals, so the effects of defaunation on plants may not be immediately obvious. Consideration of three classes of ecological interaction – seed dispersal, herbivory, and predation – suggests how floristic changes might occur in defaunated forests.

Seed dispersal

Most trees are typically dispersed by frugivorous guilds of several animal species, rather than by one co-evolved species, and most animal species consume fruit from several plant species (but see Roth, 1984, and von Roosmalen, 1985, for some important exceptions). Therefore, there is a degree of redundancy built in to most fruit/disperser systems. However, the same large animal species favoured by hunters are often the most important seed dispersers in tropical forests. So when populations of several large animal species are depleted for an extended period of time, some plant species may simply fail to regenerate. Evidence for 'dispersal breakdowns' is largely anecdotal, but nonetheless persuasive: ecologists who work in defaunated tropical forests are often struck by the obvious failure of some prolifically fruiting trees to be dispersed, as piles of uneaten fruit accumulate and rot under the parent tree, in contrast to the situation at field sites that are not affected by hunting.

Dispersal may be a critical process for maintenance of tree diversity, by removing seeds from unsafe sites crowded with conspecifics, that may, for example, attract predators or pathogens (Janzen, 1970; Connell, 1971). Numerous studies have shown the advantages of dispersal for a species' regeneration. For example, Hubbell and Foster (1990) found that saplings under conspecific adults have reduced survivorship and growth, compared with saplings dispersed a distance from conspecific adults. Chapman and Chapman (1995) estimated that up to 60% of tree species at Kibale Forest, Uganda, could fail to recruit adequately if frugivorous species were removed, based on the proportion of species that do not to regenerate freely under conspecifics. Eventually, therefore, large imbalances in populations of several frugivorous animals could eliminate populations of some trees. Since mammal-dispersed trees and lianas tend to be localized in distribution (Gentry, 1983), a localized loss of large mammalian dispersers may result in disproportionately many plant species extinctions.

Herbivory and seed predation

Research in Panama and Mexico has revealed the critical role that some herbivorous animals may have in determining the composition and diversity of tree species in the

forest. Both examples consist of comparisons of partly defaunated forest fragments with less defaunated larger fragments. They also show, incidentally, that defaunation is an inevitable consequence of fragmentation, and therefore that the lines dividing the threat categories can become very blurred.

Putz *et al.* (1990) and Leigh *et al.* (1993) found that a depleted fauna can lead to a decline in tree species richness. They surveyed islands in Panama, isolated by artificial lake-waters in 1913, that were too small to support rodent seed predators. The island forests have changed greatly, losing floristic diversity and becoming dominated by a few large-seeded species which have been released from normal levels of predator pressure. By contrast, on the nearby much larger Barro Colorado Island (BCI), population densities of important seed predators such as squirrels (*Sciurus*) and agoutis (*Dasyprocta*) have persisted at very high densities, apparently because the island is too small to support their own predators (Glanz 1982, 1990). Terborgh (1988, 1992) has suggested that the superabundance of large seed predators could be depressing the regeneration of large-seeded plants on BCI, which would be a completely contrary result to that pertaining on the smaller islands. This highlights the difficulties in predicting which animal and plant species will 'win' and which will 'lose' under different defaunation scenarios.

In a further demonstration of the importance of forest herbivores, Dirzo and Miranda (1990, 1991) made an elegant comparison of the fauna and understorey of two Mexican rainforests. One (Los Tuxtlas) is a 700 ha forest fragment which has suffered extinctions and sharp declines among its larger mammals; the other (the Lacandon rainforest in Chiapas) is far more extensive and still has near-normal mammalian populations, including the full complement of large herbivores (peccaries, tapir and deer). In the Los Tuxtlas understorey there was no sign of vertebrate browsing, the seedling density was twice as high, and the diversity of plants was much lower than in the Chiapas forest which was being browsed. Herbivory appears to be promoting the diversity of understorey plants by preventing a few species from monopolizing the physical resources, in much the same way that moderate levels of sheep grazing maintain plant diversity in British chalk grasslands (Wells, 1971), or predatory starfishes can maintain mollusc diversity in intertidal food webs (Paine, 1966). Eliminating herbivores, therefore, can not only shift the competitive balance in favour of some plants over others, but it can also reduce overall floristic diversity.

Predation

Several tropical forest studies indicate that carnivorous predators are 'keystone species' that help to structure animal communities, and thereby plant communities. In a wide-ranging comparative analysis, Emmons (1987) suggested that prey species' densities become very uneven in the absence of large felid predators, and the well-studied example of BCI confirms that predation pressure, or its absence, can have an enormous effect on prey populations. Theoretical research further suggests that loss of a few top predators will cause more knock-on extinctions in species-rich systems than would loss of a few species at lower trophic levels (Pimm, 1986).

Few tropical ecosystems retain their full natural complement of top predators. In the neotropics, for example, hunting has left populations of cat, otter, large eagle and caiman species decimated. Predicting the consequences of this for plant species is especially hard, because of the indirect effects of the top predators on plants and other animals (Terborgh, 1988), and the potential for synergisms with other ecosystem stresses. For example, if

predator populations are already suffering direct hunting pressure, human hunting of their prey species could indirectly cause extinctions among the predators, which in turn could increase the unevenness of herbivorous species' population densities, in turn altering herbivore impacts on plants.

CHANGING TREE TURNOVER RATES

Phillips and Gentry (1994) compiled data on tree turnover through time, by averaging tree mortality and recruitment rates at 40 pantropical sites. The dataset showed an overall trend toward an increase in turnover rates in the late 20th century, whether analysed as change in the annualized average rate across all inventoried forests, or as changes within 19 sites that had three or more inventories. Since then, some additional sites have come to light, and the overall pattern using updated datasets (Phillips, in press) remains largely unchanged (Fig. 2).

Why tree turnover rates have increased is not clear – indeed no large-scale observational study of ecological phenomena is easily amenable to a conclusive causal analysis – and so it is also not clear if and how turnover rates might change in the future. In our original paper we hypothesized that the increase in turnover is related to enhanced productivity, stimulated by increasing atmospheric CO₂ and I propose more possible explanations later on. In the context of this paper, the finding is most significant in demonstrating how poorly we understand the ecology of tropical forests and our impacts on them. It shows that current ground-based research programmes are still insufficient to monitor or predict, let alone help prevent, the effects of long-term environmental change on the most diverse ecosystems. In the continuing absence of a reliable science for predicting the consequences of environmental change, the finding suggests that we should take a precautionary approach and tackle the causes of environmental change sooner rather than later.

The consequences of increased tree turnover may include substantial changes in both biological diversity and the carbon cycle, since tropical forests contain globally significant stores of both diversity and carbon (Pimm and Sugden, 1994). Consideration of the role of forest dynamics in regulating diversity suggests how some biotic consequences of increasing turnover might be manifested. Empirical evidence strongly indicates that gap dynamics help to regulate diversity (Denslow, 1987), and that more dynamic forests tend to be more diverse than less dynamic forests (Phillips *et al.*, 1994b). Therefore, forests with intrinsically low turnover rates might experience an increase in local species richness, as more frequent canopy openings should permit a greater variety of species to co-exist. But turnover rates are changing in ecological, not evolutionary time, and so they cannot lead to a global increase in species diversity. A reasonable prediction is that in combination with other factors likely to favour faster-growing plants (see later), increased turnover could lead to significant losses in biodiversity both regionally and globally. In mature primary forests, the rarest, slowest-growing tree species (and some animal species, including host-specific insects and probably including other animal and plant species indirectly linked to the slowest-growing plants) may lose out to faster-growing opportunistic tree and liana species which are better suited to exploiting small gaps and unprecedented levels of atmospheric CO₂.

Annual Turnover Rates, 1957-1993

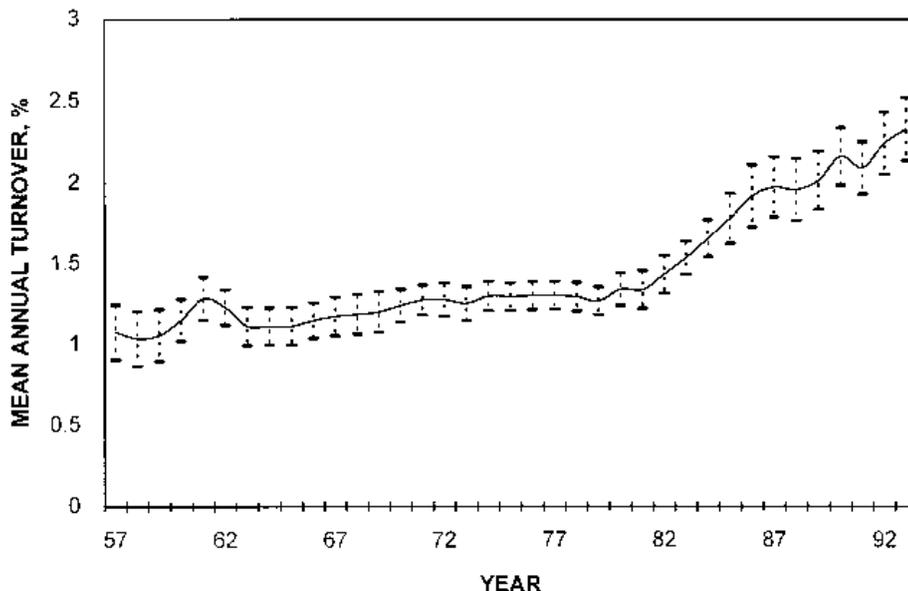


Figure 2. Annual mature tropical forest turnover rates measured since 1957. Tree turnover for each site is computed as the average of annual mortality and recruitment rates. Turnover rates are expressed as the annual mean (\pm standard error) of all simultaneously measured rates. The total number of forest sites monitored is 59; the minimum number of simultaneous monitoring sites is 8 (in 1957–9, 1993), the maximum number of simultaneous monitoring sites is 30 (in 1980). The sites used to calculate mean annual turnover rates switch through time, since few data are available for more than 20 years from any one site. Therefore, the trend could conceivably result from a progressive and very pronounced change in the kinds of forest sampled. In order to control for such an artefactual explanation, we also looked at change at forest sites with at least two consecutive measurement intervals. A large majority of the sites with successive intervals had higher turnover in later measurement intervals than in earlier measurement intervals (ratio of sites is 20:4; $z = 3.63$, $P < 0.001$, Wilcoxon matched-pair signed rank test). Further details are given in Phillips (in press).

Interactions between threats and forests

The individual threats do not operate in isolation, either from one another, or from the pervasive threat posed by outright deforestation. The overview touched on some interactions among the threats that could magnify their impact on biodiversity – for example the interactions of climate change with forest fragmentation, or of climate change with deforestation. In many cases, if the first order threats to plants and animals are themselves poorly understood, some of the higher order interactive effects between them are purely hypothetical. This section is therefore very speculative. But our poor understanding of the nature of these synergistic effects does not diminish their potential impact on the ecology of tropical forests. Interactions between one or more threats and forest ecology will be built from one or more of three basic forms (Fig. 3). In practice, these basic forms will probably be combined in various ways in complex networks of interactive cause and effect.

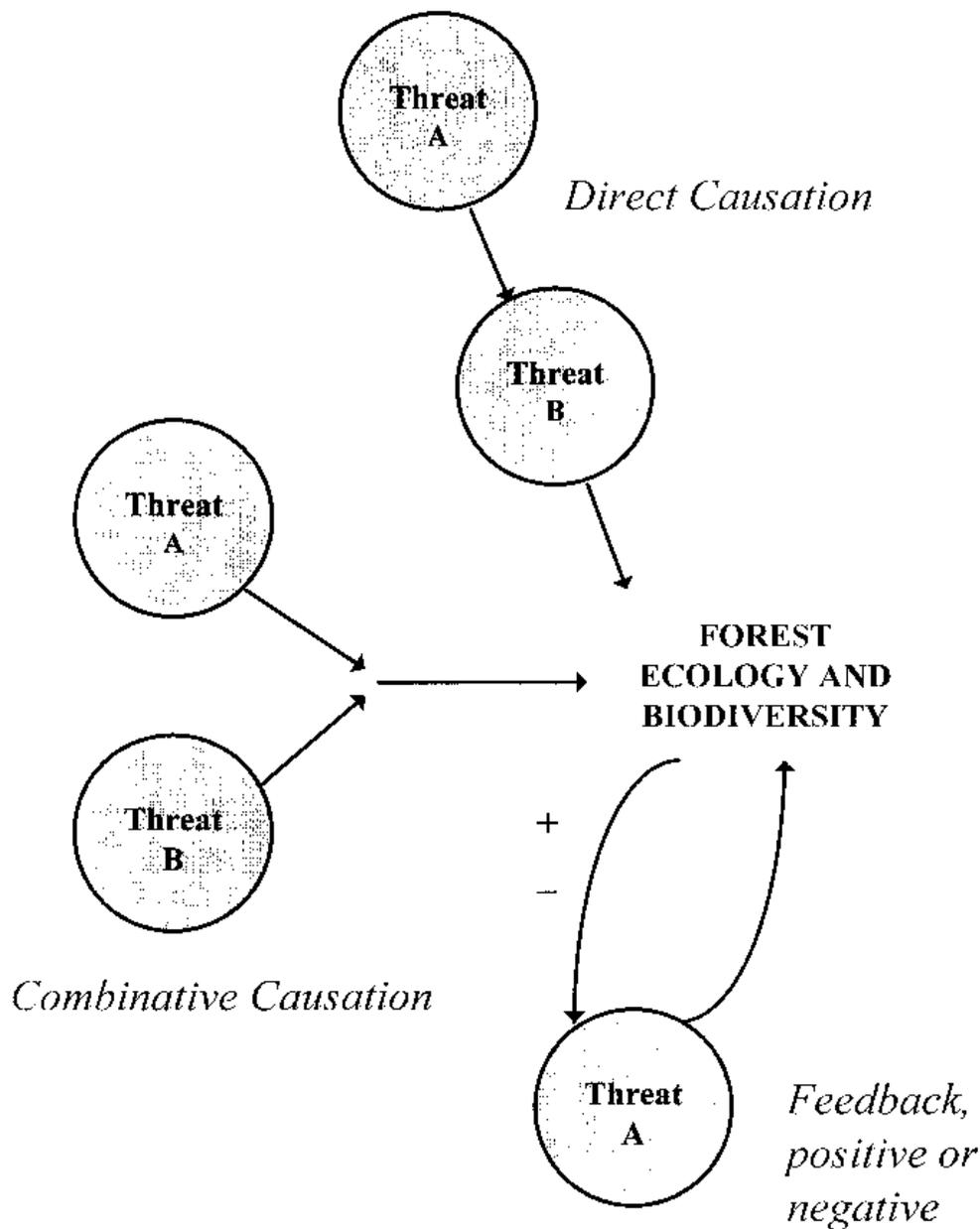


Figure 3. Three basic kinds of interaction between threats and forest ecology. See text for explanation and examples.

DIRECT CAUSATION

One of the seven direct threats to tropical forest biodiversity may also be the direct cause of another threat. For example, on a local scale, once a forest is fragmented tree mortality is enhanced close to the new forest edge, presumably due to altered exposure to physical

stress factors such as wind and low humidity associated with fragmentation (Lovejoy *et al.*, 1984; Kapos, 1989; Bierregaard *et al.*, 1992). Similarly, fragmentation alone typically causes some local animal extinctions, especially in wide-ranging rare species such as top predators. In some respects it therefore has a similar 'defaunatory' impact as hunting (c.f. 'Herbivory and seed predation' under the earlier heading 'Two invisible threats').

On larger scales, the phenomenon of recently increasing tree turnover may be explained by one or more of the other processes. Rising atmospheric concentrations of CO₂ could be enhancing primary productivity, thereby increasing the rate with which wood cycles through the community. Regional or global climate changes, in turn driven partly by deforestation and/or rising atmospheric CO₂ levels, could also affect tree turnover rates. Alternatively, hunting of large frugivores is certain to affect large-fruited animal-dispersed trees, so that trees with wind-dispersed and smaller animal-dispersed fruits could benefit from a competitive release effect. Since trees in the second group are more likely to be earlier successional plants with naturally higher rates of growth and mortality (Foster and Janson, 1985; Denslow, 1987; Swaine and Whitmore, 1988), increasing tree turnover rates might partly be a result of shifts in tree species composition caused by the widespread hunting of the largest tropical forest frugivores.

COMBINATIVE CAUSATION

Interaction between two or more processes may also generate an impact on biodiversity different from that caused by either alone. For example, low-level hunting pressure could trigger extinctions among otherwise viable animal populations persisting in forest fragments. Smaller fragments are also relatively more susceptible to biological invasion by alien species or by species more typical of successional habitat (Janzen, 1983). An otherwise sustainable level of selective cutting of fruit trees, combined with an otherwise sustainable level of hunting of its major dispersers, could together eliminate several animal and plant species, particularly if the fruit trees also happen to be keystone resources for animals during seasons of scarcity (Howe, 1984; Terborgh, 1986). Logging (selective extraction of plants) combined with drought (likely to become more frequent and more intense as global warming proceeds) may make otherwise unburnable humid forests vulnerable to fire.

It is also possible that some threats to biodiversity might help defuse, or reverse, the impact of other threats. Brazil nut tree (*Bertholletia excelsa*) seeds are extracted from forests in large quantities by humans and dispersed by rodents (agoutis); new data from Peru (Enrique Ortíz, pers. comm.) suggest that moderate levels of some human activities (including small-scale forest disturbance, and perhaps hunting of large predators) will lead to increased agouti populations. *Bertholletia* regeneration may therefore be improved in those areas where humans are collecting seeds relative to areas where human impact is minimal. *Bertholletia* regeneration may also be boosted by unintentional seed scattering by collectors, and by other human activities that create small light gaps.

FEEDBACK

In the third kind of interaction between threats and forest ecology, the individual processes either feed on themselves in a 'vicious circle' of positive feedback, thereby magnifying the impact on biodiversity, or eventually moderate themselves in a 'virtuous circle' of negative feedback. For example, increasing turnover may lead to greater opportunities for

colonization by fast-growing tree species that regenerate preferentially in light gaps, which in turn have intrinsically higher mortality rates than more shade-tolerant species (Swaine and Whitmore, 1988). The result could be a further increase in tree turnover. The direct, physiological effects of increasing atmospheric CO₂ are more likely to benefit intrinsically fast-growing species, boosting stem turnover rates further. Lianas may benefit from the more dynamic and resource-rich environment, and their growth would be likely to accelerate tree mortality further (Putz, 1982), thereby further generating conditions that suit their own growth. This hypothetical positive feedback cycle could then directly cause other threats to biodiversity. For example, any shift to faster-growing plants may result in net loss of carbon from both living biomass (fast-growing species are less dense than slow-growing species, and younger trees are less dense than their older conspecifics (Castro *et al.*, 1993)) and from detrital carbon (Cebrián and Duarte, 1995). Primary tropical forests could therefore become net sources of atmospheric CO₂. That, in turn, could have ecosystem and biome-level effects via climate change.

In other, more optimistic scenarios, negative feedback imposes an upper limit on the biotic impact of individual processes. For example, if lianas do benefit at some point they will approach saturation of their trellis resource (suitable tree species), thereby halting liana population growth. Another negative feedback effect might begin to modify hunting pressure on animals once target populations fall below a certain level. Thus, human hunters who are maximizing their time allocation to hunting effort may conclude that it is no longer worth trying to hunt these now rare animals. This could result in sharply decreasing pressure on animal population densities as they fall below critical thresholds, and perhaps allow them to survive indefinitely – albeit as newly rare species newly vulnerable to stochastic events that could cause their extinction.

Potential outcomes for plants and animals

How might the forests of the future compare with those of the recent past? Predicting the biotic impacts of poorly understood changes on complex systems is hardly straightforward! However, some general effects on biodiversity resulting from these non-deforestation threats can be anticipated with some confidence, from basic ecological principles, unless preventative and remedial actions are taken. As we saw earlier, rare species and habitat specialists are particularly vulnerable to extinction and should therefore be priorities for conservation and monitoring (Terborgh and Winter, 1980). Other common-sense predictions can also be made. Table 1 indicates hypothetical population changes among some broadly defined groups of organisms in tropical forests. When these are compared for each group across all the threat classes, some groups of organisms appear likely to do consistently badly, others consistently well. For example, some large-seeded tree species dispersed by large herbivores are predicted to be at a relative disadvantage from every one of the threats. Small-seeded, wind-dispersed tropical vines, on the other hand, seem destined to prosper as a result of most of the changes.

This crude tally is offered as a first step toward indicating which groups of plants and animals might most require intervention by conservationists. Obviously, these suggestions should be treated with caution. For one, even among groups that are predicted to benefit as a whole, it is possible that non-deforestation extinctions will still occur. Most importantly, this approach does not take into account all the potential higher-order interactions among threats, simply because they are so hard to predict. In some cases these

Table 1. Hypothetical population changes among native forest organisms in response to threats

Threat	Trees				Lianas and vines				Animals			
	Dispersed by large animals		Dispersed by wind or small animals		Dispersed by large animals		Dispersed by wind or small animals		Carnivores		Herbivores	
	large seed	small seed	large seed	small seed	large seed	small seed	large seed	small seed	large	small	large	small
A	-1	-1	?	?	-1	?	+1	+2	-1	?	-1	?
B	-2	-2	+1	+2	-2	-2	+1	+2	-2	+1	-2	+2
C	-1	-1	-1	-1	?	?	?	?	?	?	-1	-2
D	-2	-2	?	+2	-2	-2	?	+2	-2	?	-2	+1
E	-1	-1	?	?	-1	-1	?	?	-1	?	-1	?
F	-1	+1	-1	+1	?	+1	+1	+2	-1	?	-1	+1
G	-2	?	-1	+1	?	+1	?	+2	-1	?	-1	+1
Sum	-10	-6	-2	+5	-6	-3	+3	+10	-8	+1	-9	+3

A = Selective extraction of plants (especially felling trees).

B = Selective extraction of animals (especially hunting animals).

C = Biological invasion.

D = Fragmentation (including isolation of populations, and enhanced edge effects).

E = Climate change (especially increased drought).

F = Atmospheric change (especially increased CO₂ levels).

G = Increasing tree turnover.

? = Effect, if any, as likely to be positive as negative.

+1 = Possibly benefiting (i.e. if any effect, more likely to benefit than suffer).

+2 = Probably benefiting.

-1 = Possibly suffering (i.e. if any effect, more likely to suffer than benefit).

-2 = Probably suffering.

effects could switch the balance of winners and losers. For example, large-seeded trees could still benefit, if they also have good intrinsic defence mechanism against climbers. Palm trees, which usually remain free of climbers, and some myrmecophilous plants – which provide ant species with a home in return for their protection against various biotic threats – are some candidates for ‘surprise winners’ as forest ecosystems change in reaction to externally driven processes.

These considerations lead to some practical suggestions for future monitoring and conservation in tropical forest reserves. There is an urgent need for a greater emphasis on monitoring liana populations (Gentry, 1991; Hegarty and Caballé, 1991) which are overlooked in at least 90% of permanent inventory forest plots. Many lianas are likely to benefit in degraded forests by virtue of their opportunistic life-history characteristics. Since some animals and plants are disproportionately likely to suffer as primary forests become degraded, lists of ‘most-at-risk’ species and ecological guilds would also be useful guides for monitoring and conservation programmes. If major ecological imbalances are suspected, there would be a case for conservationists to take an interventionist approach to correct the imbalance. Examples might include culling seed predators that no longer have

natural predators, and enrichment planting with plant species that are outcompeted by other plant species under an altered herbivore regime. Such intervention will surely involve intense scientific and ethical debate, but may become increasingly necessary.

Conclusions

Change and disturbance in tropical forests is not necessarily harmful. Small and large disturbances (tree-falls, cyclones, droughts, and so on) are part of the natural regime, and even those areas that today apparently support pristine forest communities have been the sites of occasional human activity for thousands of years. So long-term biological degradation is not an inevitable consequence of human impact, and all biologists would probably agree that even a degraded forest is better than no forest at all. Moreover, the time-scales on which these threats impact biodiversity may make them less immediately dangerous than deforestation. Small patches of primary forest may maintain surprising numbers of plant species for decades or centuries in the face of various threats (Dodson and Gentry, 1991; Turner *et al.*, 1994); this time window may prove to be a critical help for conservation rescue efforts. However, this paper has shown that the current level of non-deforestation impacts on forests has already caused substantial biodiversity losses in many tropical localities, and that worse is to come.

The causes of forest degradation are dangerous in part because their biological effects are invisible from above. This makes them difficult for scientists to monitor and gives them little public salience; therefore they are easily overlooked. We must not forget that 'the functioning of rainforests depends on innumerable intricate relationships Tropical foresters and reserve designers can not afford to ignore them.' (Leigh *et al.*, 1993). It is these intricate relationships, more than simply their lush vegetation and tall trees, which help give tropical forests their special aura of mystery and vitality. As tropical forests degrade, these relationships quietly dissolve and simplify, and so eventually forests may be destroyed from the inside out rather than from the outside in. We must therefore make a critical distinction between monitoring deforestation, which mostly requires coordinated application of remote-sensing technology, and monitoring biological degradation, which will require long-term human and financial investments in field research at a large network of sites. Furthermore, in seeking to improve human standards of living while slowing outright deforestation (for example, by supporting 'extractive reserves' and indigenous peoples' land tenure rights), the conservation movement should not lose sight of the need to invest in large protected areas that are insulated from as many threats as possible.

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